

Part 1

# **SINGLE-SPECIES POPULATIONS**

### 1.1 Introduction

This book provides an introduction to the study of populations of animals and plants. Individual species are products of organic evolution that, in a multitude of differing assemblages, make up the communities of living organisms that are found on Earth. That these communities display changes in the relative abundance of species is evident both from the fossil record and in the present day. Populations of member species in a community may show a range of dynamic patterns. For instance, over time, populations may change in size relative to one another; conversely, they may show apparent constancy in size despite the fact that births and deaths of individual organisms occur continually within them. Furthermore, individuals within populations may group together in differing spatial arrangements which may change with time, even though total population size may remain constant.

Clearly changes in population size in space and time, even in simple communities, have the potential to be, and indeed often are, very complex and pose a wealth of ecological questions. For instance in a grassland community (Fig. 1.1) we may ask 'Which processes contributed to a decline in one species (*Festuca ovina*) to a quarter of its original abundance, during which time another species appeared (*Hieracium pilosella*), only to then decline with the subsequent increase of a third (*Thymus drucei*)?' Or in the case of Fig. 1.2, 'Why is there an apparent underlying regularity in the cyclical abundance of the lynx and snowshoe hare?' If we are to understand such patterns and be able ultimately to predict changes in them, then our initial focus must be on the individual species themselves and the manner in which populations respond to internal and external ecological factors. With this knowledge we may then begin to investigate questions of species-habitat interrelationships and

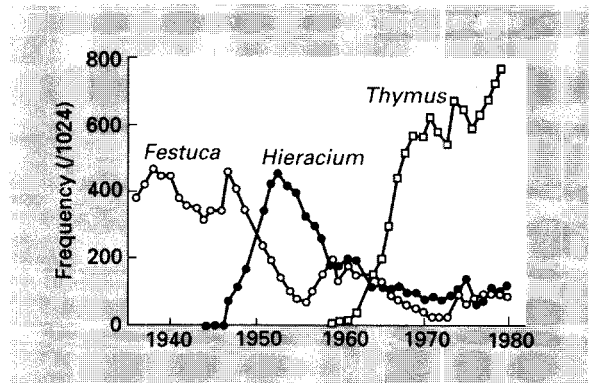


Fig. 1.1 Changes in the frequency of three species in a natural grassland community in the UK over 40 years. (After Davy & Jeffries, 1981.)

interactions among species within and between trophic levels.

This chapter is concerned with describing single-species populations and with abstracting the underlying demographic features that are common to them all. With the appropriate description, we may then be able carefully to consider the underlying causes of the dynamics of single-species populations.

### 1.2 Population processes

Although studies of animal and plant populations have developed quite separately, these two life forms have much in common when examined from a demographic viewpoint. At the simplest level, plants are born from seeds just as birds are born from eggs; and old animals exhibit signs of senility just as old oak trees bear dead branches. Moreover, if we were to catalogue the ages of every dandelion plant and every vole living in a field, we would probably find a range of ages in each; and, as time passes, individuals would either die, or survive to reach the next age group; and in some age groups, at certain times, individuals

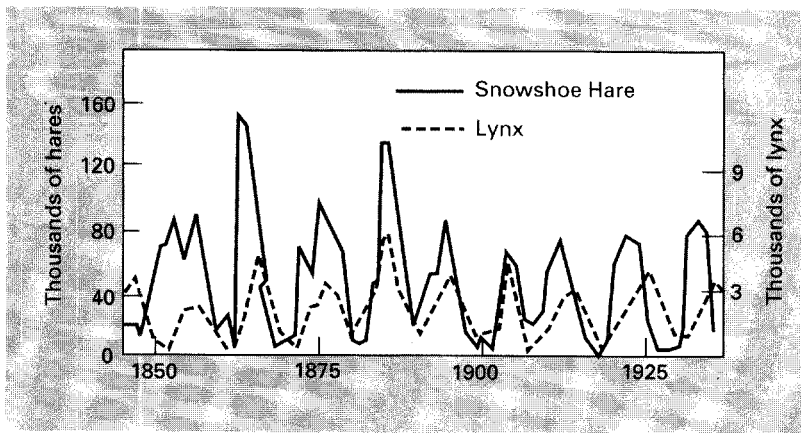


Fig. 1.2 Changes in abundance of the lynx *Lynx canadensis* and the snowshoe hare *Lepus americanus* (after MacLulich, 1937) in Canada over 80 years.

would produce offspring of their own. From the outset, therefore, it would seem sensible to suggest that, even though life forms and stages of development will differ substantially between species and across kingdoms (a point taken up in section 1.6) certain basic *population processes* are common to all of them.

We can start considering these population processes by imagining a study of the numbers of voles inhabiting a meadow. Let us suppose that the vole numbers increase. We know that there has *either* been an influx of voles from adjoining meadows, *or* young voles have been born, or both of these events have occurred. We have, therefore, pin-pointed two very basic processes which affect the size of a population: *immigration* and *birth*. Conversely, if vole numbers decline, then our explanation would be that voles must have either died, or simply left the meadow, or both. These processes, which reduce population numbers, are *death* and *emigration*.

Of course, there is no reason to suggest that all four processes are not occurring simultaneously in the population and there is therefore a flux of individuals within it. If the population declines, then the reason is simply that death and emigration together have *outweighed* birth and immigration, and vice versa if the population increases. We can certainly say that birth, death, immigration and emigration are the four fundamental demographic parameters in any study of population dynamics. Moreover, they can be combined in a simple algebraic equation describing the

change in numbers in a population between two points in time.

$$N_{t+1} = N_t + B - D + I - E \quad (1.1)$$

where  $N_t$  is the population size (number of individuals) at time  $t$ ,  $N_{t+1}$  is the population size one time period later, at time  $t+1$ ,  $B$  is the number of new individuals born between  $t$  and  $t+1$ ,  $D$  is the number of individuals which die between  $t$  and  $t+1$ , and  $I$  and  $E$ , respectively, are the numbers of immigrants and emigrants during the same period of time. One of the simplest ways of envisaging equation 1.1 is as a graphical plot of the population size at time  $t+1$  against the size of the population at a previous time  $t$ , where the time interval is one generation. This is illustrated in Fig. 1.3. If population size remains static over generations, then the population will be represented as a stable locus in graphical space on the diagonal line bisecting the graph. However, if population size changes over generations then a trajectory of loci may occur away from the equilibrium line. We will use this graphical approach to develop models of single species dynamics later after we have considered the ways in which populations can be described.

If the population is so large that our study cannot encompass the whole of it, then this equation must be constructed in terms of densities rather than absolute numbers. Thus, samples are taken, and  $N_t$ , for instance, becomes 'the number of plants per square metre at time  $t$ ' or 'the number of insects per leaf'.

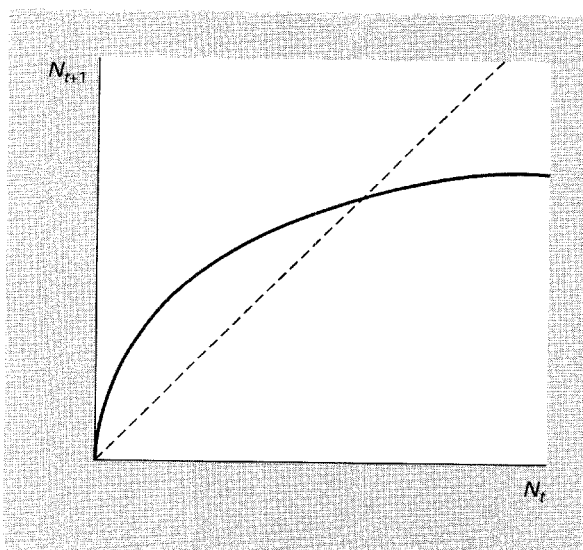


Fig. 1.3 Graphical representation of changes in population size over generations. Each successive population size  $N_{t+1}$  is plotted against starting population size  $N_t$ . See text.

Nevertheless, equation 1.1 indicates that, at its simplest, the task of the demographer is to measure these four parameters and account for their values—yet the translation of this into practice is rarely straightforward. Almost all species pass through a number of stages in their life cycle. Insects metamorphose from eggs to larvae to adults, and some have a pupal stage as well; plants pass from seeds to seedlings and then to photosynthesizing adult plants, and so on. In all such cases the different stages must be studied individually. Also, in reality, the four ‘basic’ parameters are themselves often compounded from several other component processes. Equation 1.1, therefore cannot be considered as anything more than a basis upon which more realistic descriptions can be built.

### 1.3 The diagrammatic life table

#### 1.3.1 General form

The description we require is one which retains the generality of equation 1.1, but can also reflect the complexities of most actual populations. One such description is the *diagrammatic life table* (Sagar &

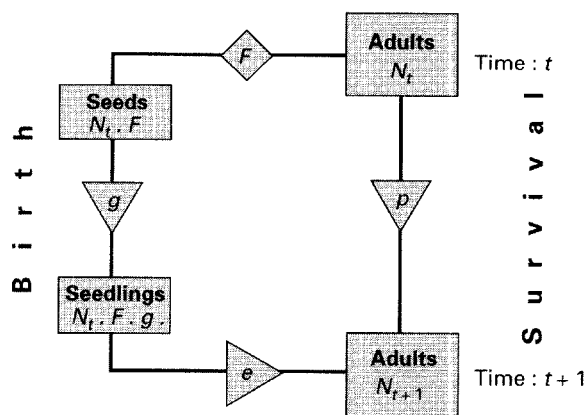


Fig. 1.4 A diagrammatic life table for an idealized higher plant.  $F$ , number of seeds per plant;  $g$ , chance of a seed germinating ( $0 \leq g \leq 1$ );  $e$ , chance of a seedling establishing itself as an adult ( $0 \leq e \leq 1$ );  $p$ , chance of an adult surviving ( $0 \leq p \leq 1$ ).

Mortimer, 1976), which is applied to an idealized higher plant in Fig. 1.4. The numbers at the *start* of each of the stages—seeds, seedlings and adults—are given in the square boxes. Thus, the  $N_{t+1}$  adults alive at time  $t+1$  are derived from two sources. Some are the survivors of the  $N_t$  adults alive at time  $t$ . Their probability of survival (or, equivalently, the proportion of them that survive) is placed inside a triangle (or arrow) in Fig. 1.4, and denoted by  $p$ . So, for instance, if  $N_t$  is 100 and  $p$  (the survival-rate) is 0.9, then there are  $100 \times 0.9$  or 90 survivors contributing to  $N_{t+1}$  at time  $t+1$  (10 individuals have died; the mortality-rate  $(1 - p)$  between and  $t+1$  is clearly 0.1).

The other source of the  $N_{t+1}$  adults is ‘birth’, which in the present case can be viewed as a multi-stage process involving seed production, seed germination and the growth and survival of seedlings. The average number of seeds produced per adult—the average *fecundity* of the plant population—is noted by  $F$  in Fig. 1.4 and placed in a diamond. The total number of seeds produced is, therefore  $N_t \times F$ . The proportion of these seeds that actually germinate on average is denoted by  $g$ , which, being essentially a survival-rate, is placed in an arrow in Fig. 1.4. Multiplying  $N_t \times F$  by  $g$  gives us the number of seedlings which germinate successfully. The final part of the process is the

physiological establishment of seedlings as independently photosynthesizing adults. The probability of surviving this very risky phase of plant growth is denoted by  $e$  (once again in an arrow), and the total number of 'births' is, therefore,  $N_t \times F \times g \times e$ . The number in the population at time  $t + 1$  is then the sum of this and the number of surviving adults,  $N_t \times p$ .

We can now substitute the terms from the life table into our basic equation of population growth (equation 1.1) as follows:

$$N_{t+1} = N_t - \underbrace{N_t(1-p)}_{\text{Death}} + \underbrace{N_t \times F \times g \times e}_{\text{Birth}} \quad (1.2)$$

There are several points to note about this equation. The first is that both here and in Fig. 1.4 immigration and emigration have, for simplicity, been ignored, and our description of how a plant population may change in size is essentially incomplete. The second is that 'death' has been calculated as the product of  $N_t$  and the mortality-rate  $(1-p)$ —survival and mortality are opposite sides of the same coin. The third point is that birth is quite clearly a complex product of 'birth-proper' and subsequent survival. This is frequently the case: even human 'birth' rates are the product of the rate at which fertilized eggs implant in the womb and the rate of prenatal survival.

### 1.3.2 The common field grasshopper, an annual species

In practice, careful and meticulous field-work is necessary to build a diagrammatic life table of the type illustrated in Fig. 1.4. Reliable estimates of the transition probabilities ( $p$ ,  $g$  and  $e$  in Fig. 1.4) are required, as well as measurements of the fecundity of adults. Such data for the common field grasshopper, *Chorthippus brunneus*, are illustrated in Fig. 1.5. These were obtained by a combination of field samples and back-up laboratory observations on a population near Ascot in Berkshire (Richards & Waloff, 1954). The population was isolated so that immigration and emigration could be ignored.

The first point to note about Fig. 1.5 is that no

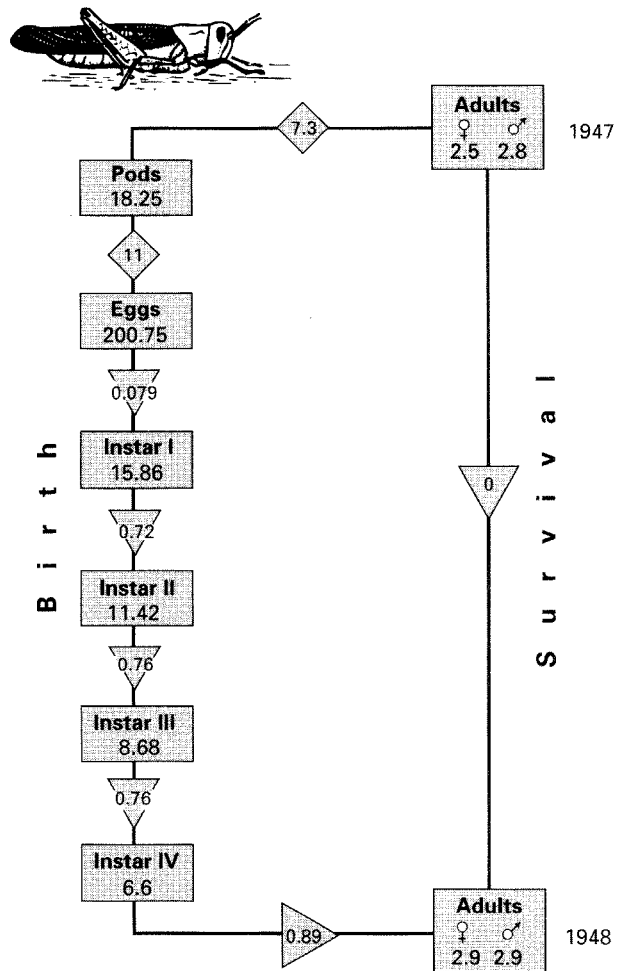


Fig. 1.5 Diagrammatic life table of the field grasshopper *Chorthippus brunneus*. (Population sizes are per  $10 \text{ m}^2$ ; data from Richards & Waloff, 1954.)

adults survive from one year to the next ( $p = 0$ ). *Ch. brunneus* is, therefore, an 'annual' species; each generation lasts for just 1 year, and generations are discrete, i.e. they do not overlap. It is also clear that the 'birth' of adults is a complex process involving at least six stages. The first stage is the laying of egg-pods in the soil by adult females. On average, each female laid 7.3 pods, each containing 11 eggs.  $F$  is, therefore, 80.3. These eggs remained dormant over winter, and by early summer only 0.079 of them had survived to hatch into first-instar nymphs. Subsequently, the transition probabilities between instars were fairly

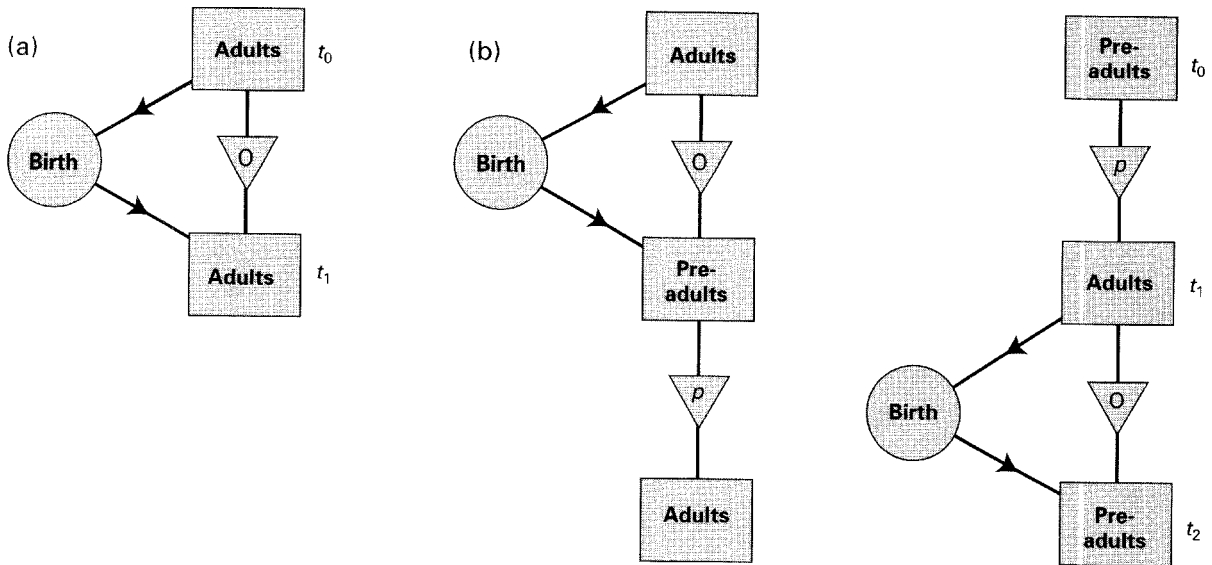


Fig. 1.6 Diagrammatic life tables for species with discrete breeding seasons. (a) Generations do not overlap. (b) Generations overlap. (Birth processes are simplified.)

constant, taking a remorseless toll on the surviving population; less than a third of the first-instar nymphs survived to be 'born' into the adult population. Despite their apparently high fecundity, therefore, the adults of 1947 did little more than replace themselves with newly born adults in the following year.

The *Ch. brunneus* diagrammatic life table is illustrated in a simplified form in Fig. 1.6a. This life table is appropriate for all species which breed at a discrete period in their life cycle, and whose generations do not overlap. If the time between  $t_0$  and  $t_1$  is 1 year, the life history is referred to as annual.

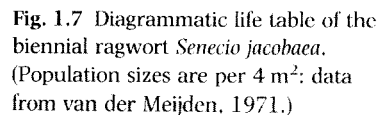
### 1.3.3 Ragwort, a biennial

An annual life history is only one of a number of possible patterns. If we consider species that live for 2 years rather than 1, reproducing only in the final year, then we have a life history that involves breeding at one discrete time in the life cycle, but in which generations of adults may well overlap; this is illustrated in Fig. 1.6b. If the time periods are years, then this life cycle is referred to as 'biennial'. During any

one summer, the population contains both young adults which will not reproduce until the following year, and mature, reproducing adults.

Ragwort, *Senecio jacobaea*, is a biennial plant with a life cycle in which seeds germinate principally in the autumn. Then, during the next year, young plants form a rosette of leaves. In the second year a flowering stem is formed. A diagrammatic life table for *S. jacobaea* is shown in Fig. 1.7, in which the birth process has been expanded to include some extra stages which are specific to plants. The data come from measurements made on a population living in sand dune environments in the Netherlands (van der Meijden, 1971). Of the 5040 seeds that are produced, 62% fall on to the ground; the other 38% are dispersed by the wind to other areas. By the same token there is quite a high chance that immigrants enter this population. This necessitates a further modification of our life table, indicated in Fig. 1.7 by the inclusion of invading seeds, which may contribute either to the seed banks or to the incoming seed 'rain'.

Having arrived on the ground, various potential fates await ragwort seeds. They lie on the surface of the sand in the 'surface seed bank', where they may germinate, be eaten or just die. Alternatively, wind or insects, acting as migratory agents, may transport them to neighbouring areas; or they may become



seeds that rain on to the soil only 40 actually germinate successfully. However, seedlings can arise from an additional source: the buried seed bank. We

do not know how many seeds are buried in the sand profile, but for many plant species, especially weeds, the numbers of buried seeds can be very high (up to c. 50 000 m<sup>-2</sup>), and a proportion of each season's seed crop does become buried. To indicate that this is a birth route we have added to the 'seedling' and 'established plant' components a fraction of the buried seed bank, denoted by *S*. Finally, the transition from seedlings to young, established, photosynthetically independent adults in sand dune environments is also an exceedingly risky phase for ragwort: only 1.7% of the seedlings actually become established.

The life table in Fig. 1.7, therefore, illustrates the importance of additional seed sources to the 4 m<sup>2</sup> area, since from *t*<sub>0</sub> to *t*<sub>1</sub> the original ragwort density of 1 becomes reduced to 0.69. Thus, to keep the number of young adults at *t*<sub>1</sub> up to exactly 1 we might argue that there are 155 seeds in the buried bank which germinate (since if  $0.69 + 0.002S = 1$ , then  $S = 155$ ). Alternatively, some of these 155 might enter the 'birth process' as immigrants; and if we recall that 38% of the 5040 seeds were dispersed, we can see that there are ample numbers to rely upon. To complete this life table, however, we should note that the chance of a young adult surviving to become a mature one *producing seed* is only 0.25. To ensure that the population size at *t*<sub>2</sub> is still 1, therefore, we will have to imagine a further input of seeds into the birth process.

Such data as these emphasize the extreme severity of the sand dune habitat to plant life, and the considerable mobility of seeds in the life cycle of ragwort: individual seeds may travel at least 15 m. Since sand dunes, by their nature, offer shifting and temporarily suitable habitats for ragwort, we can infer that seed movement by dispersal on or above the sand is a very necessary feature in the life of this plant.

### 1.3.4 More complex life cycles

Overlapping generations are not confined to biennials. Consider the population of great tits (*Parus major*) near Oxford studied by Perrins (1965) and illustrated in Fig. 1.8. Adult birds build their nests and lay eggs in the early summer, but of these eggs only a proportion (0.84 in this case) survive to hatch as nestlings. These

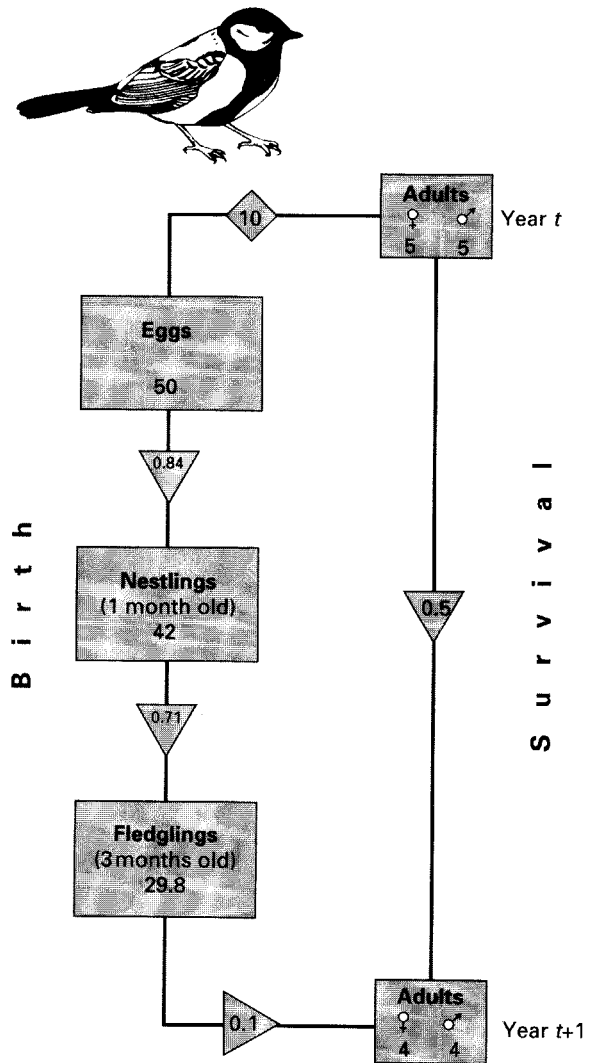


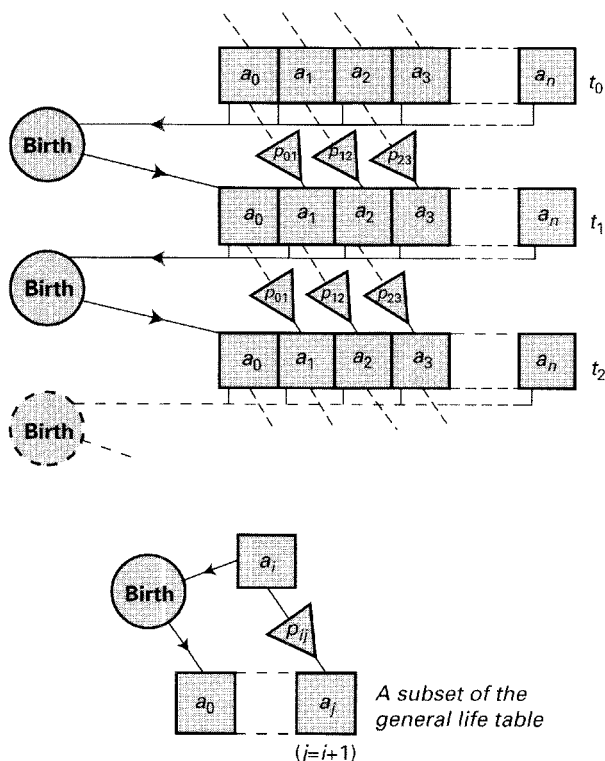
Fig. 1.8 Diagrammatic life table of the perennial great tit *Parus major*. (Population sizes are per hectare: data from Perrins, 1965.)

nestlings are themselves subject to many dangers, and by the late summer only 71% of them survive to fledge—leaving the nest and fending for themselves. Of these fledglings, only a small proportion live through the winter to become breeding adults. However, a rather larger proportion of the previous generation's adults have also survived. The population of breeding adults, therefore, consists of individuals of various ages, from 1 to 5 or more years old. As Fig. 1.8 shows,



this situation is readily described by a variant of our diagrammatic life table very similar to Fig. 1.4. We are dealing with a population in which breeding occurs at discrete time periods, but in which the individuals are potentially long lived so that *many* generations overlap.

We have assumed with our great tits, however, that adults of different ages are equivalent and may be treated as equal members of a common pool. Yet there will be many instances in which their demographic characteristics will be 'age-dependent' or 'age-specific'. In such cases, a diagrammatic life table of the type shown in Fig. 1.9 may be more appropriate. In



**Fig. 1.9** A diagrammatic life table for any species that reproduces continuously with overlapping generations.  $a_0, a_1 - a_n$  represent age groups of individuals,  $a_n$  being the oldest group.  $p_{ij}$  is an age-specific probability of survival, where, for example,  $p_{01}$  the probability of individuals in  $a_0$  at one time surviving to reach  $a_1$  by the next time period ( $0 \leq p_{ij} \leq 1$ ). The inset shows a subset of the general life table.

Fig. 1.9, the population at any one time consists of individuals in a range of age classes:  $a_0$  individuals are in the youngest age-class,  $a_1$  individuals in the next oldest, and so on. With the passage of one unit of time a proportion of the individuals in one age group survive to become individuals in the next oldest age group. Thus  $p_{01}$  is the proportion of the  $a_0$  individuals surviving to become  $a_1$  individuals one time unit later,  $p_{12}$  is the proportion of the  $a_1$  individuals surviving to become  $a_2$  individuals, and so on (though in practice these  $p$ -values will, of course, vary with the changing circumstances of the population). Figure 1.9 also shows that each age group has the potential to contribute to the youngest age-class via the birth process. For simplicity, birth from all age groups has been fused together; in reality, fecundity, like survival, would vary from age-class to age-class. Nevertheless, despite this increased sophistication, inspection of the life table in Fig. 1.9 reveals that it is built up of units which are little more than the diagrammatic life table with which we are already familiar. One such unit is illustrated in the inset in Fig. 1.9.

The implication in Fig. 1.9 is that breeding occurs at discrete periods, even though generations overlap and there are many age-classes each with their own birth- and survival-rate. In many species, however, birth (and death) occur continuously within a population. Figure 1.9 is still appropriate in such cases, but time must be split arbitrarily into intervals, and the various terms take on slightly different meanings. Suppose, for instance, that we consider the numbers in a population at monthly intervals. At  $t_0$ ,  $a_2$  is the total number of individuals between 2 and 3 months old. One month later (at  $t_1$ ),  $p_{23}$  of these will survive to become the  $a_3$  individuals that are between 3 and 4 months old. Thus, even though birth and death are occurring continuously, they are considered 'one month at a time'.

### 1.3.5 Age and stage: the problems of describing some plant and animal populations

Figure 1.9 illustrates the age-dependent transitions that may occur in populations with overlapping generations. As a means of describing flux in populations,

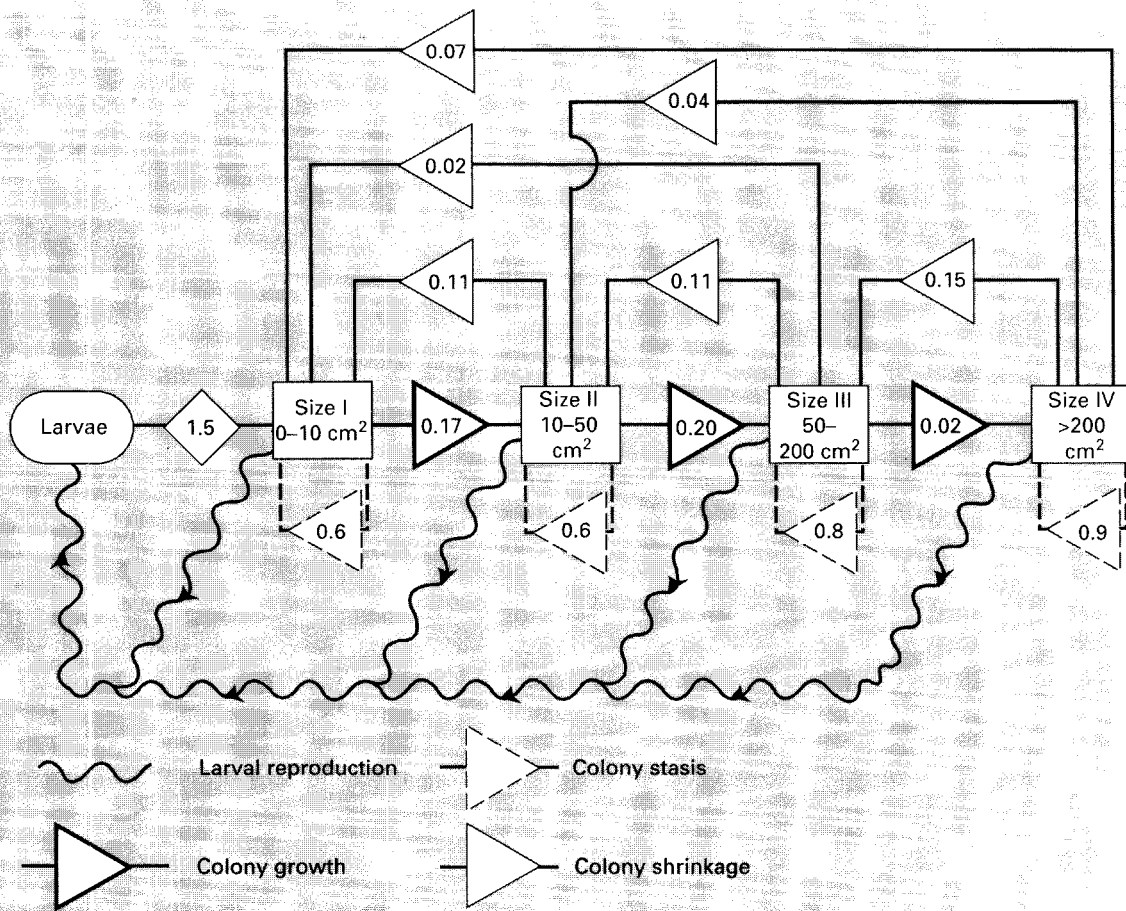
this approach is only justifiable if individuals can be classified meaningfully by *age* alone. For many plant species, however, especially those that are perennial, the fate of an individual is not so much dependent on its absolute age as on its size or stage of growth. In grasses, for instance, the chance of being grazed may be crucially size-dependent, and an individual with a few tillers may escape the notice of a herbivore whilst a conspicuous one bearing many tillers may not. Equally important is the fact that the grazed individual, though reduced in size, may not necessarily die, but may generate from basal growing points (buds) to achieve its former size. Age of the plant under such circumstances may have little relevance. Size of the plant is the more important determinant of its fate. Considerations of this sort have led a number of plant ecologists, particularly in the Soviet school (Gatsuk *et al.*, 1980) to reject age *per se* in favour of 'age states' as a useful criterion for describing individuals (Uranov, 1975; see Silvertown, 1982 for a worked example). Thus, individuals may be classified on an ontogenetic or developmental basis and categories might include seed, seedling, juvenile, immature, virginile, reproductive, subsenile and senile states. Such a classification recognizes that there are broad morphological changes that occur during the growth and development of a plant species but that the duration of time spent in each may differ widely. Mertz and Boyce (1956), for instance, have shown that almost 75% of the oak tree 'seedlings' developing after a forest felling were in fact sprouts attached to roots up to 40 years old. Presumably this 'seedling' population had remained suppressed at an early stage or 'age state' due to factors such as grazing, trampling and poor conditions for growth.

An alternative classification of individuals is by size alone and indeed this can be superimposed upon an age-state classification. Terrestrial plants that can 'reiterate' their growth form (see section 1.6) can not only regress or advance from one age-state to another, but within an age-state they may also change in size. The choice between a strictly size-based and an age-state classification, or indeed a hybrid between the two, is very much dependent upon the organism under study.

In studying the population dynamics of reef coral *Agaricia agaricites*, off the coast of Jamaica, Hughes (1984) classified individual coral colonies on the basis of age-state—'larva' or 'coral colony'—and on the size of colony. By repeated photography of the reef he was able to record size changes as well as larval recruitment. A diagrammatic representation of the population structure is shown in Fig. 1.10. Coral colonies may remain static in size, they can grow, they can shrink, and they can reproduce sexually by free-swimming larvae as well as asexually by fission. The chances of their doing so for each size-class are shown in this figure, for a year when storms were absent and conditions ideal for coral growth. This coral species has a mean annual lateral extension rate of less than 2 cm. Thus, a large proportion of the population remained in the same size-class from one season to the next. Moreover, whilst only a small fraction of the colonies increased in size, a more likely occurrence was that they should shrink to smaller size-classes, a fate moreover that was size-dependent. This shrinkage may represent a series of remorseless steps towards mortality of the individual, but equally it may also reflect fission of the colony and hence asexual reproduction. Indeed, in the case of size-class 4, it must do so since the sum of the fractional transitions exceeds unity.

This sort of description, based primarily on size alone, has limitations in so far as it does not readily distinguish between survival and fecundity, especially when asexual reproduction is involved. Moreover, in the majority of classifications of this type, at least one additional category, as we have already mentioned, must be included to complete the life cycle: larvae. Hughes recorded 1.5 larvae  $m^{-2}$  settling as new recruits during a year in his study. In *Agaricia* the probability of reproducing sexually by larvae is unknown (Connell, 1973), but even if size-specific fecundities were measurable, they might have little value in describing the local populations of this coral since larvae tend to be very widely dispersed. Using this figure for larval recruitment, Hughes was able to calculate by matrix methods (see Chapter 3) that the population was almost static in size.

A comparable approach describing a plant species is



**Fig. 1.10** A size-based diagrammatic life table for the reef coral *Agaricia agaricites* growing in calm seas. (Data from Hughes, 1984.)

the one used by Sarukhan and Gadgil (1974) for the 'creeping buttercup', *Ranunculus repens* in Britain. This species reproduces sexually by seed and by asexual propagation, though recruitment by these means occurs at different times during the season. Seeds germinate in late spring and early summer, whilst in late summer new 'daughter' plants become established as separate adult plants from shoots borne at nodes along creeping stolons. If we require a description of these events within a season, and hence

a more faithful representation of the biological events that occur, we must recognize that the generalized life-table diagram is inadequate and accept a more complex flow diagram (Fig. 1.11). In essence this is an age-state classification in which the fluxes are precisely defined chronologically. This approach makes an additional important distinction, in that asexually produced 'vegetative' daughters are classified separately from sexually produced seedlings, at least during the first year of life. For the purposes of generality, Sarukhan and Gadgil lumped these recruits together once they attained 1 year of age, but there is no reason why this distinction could not be maintained if continued resolution was required.

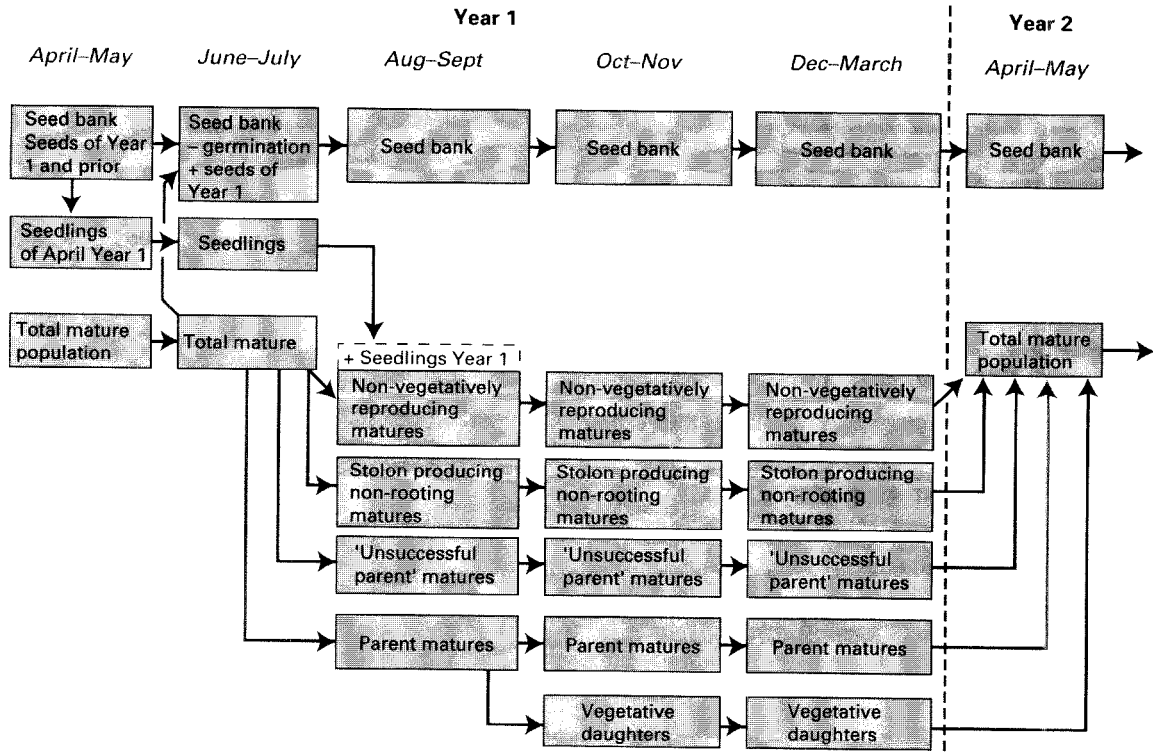


Fig. 1.11 The transitions occurring throughout the year in a buttercup population (*Ranunculus repens*) as envisaged by Sarukhan and Gadgil (1974).

In describing populations by diagrammatic means, then, we have considered a range of forms of description. Some have been based on generation-to-generation changes classifying by age, while others have been based on size taking for convenience season-to-season or month-to-month time-steps. In this latter instance, it is easy to preclude particular life-cycle transitions (if the biology of the species demands this) by setting them to zero.

Additionally, we can impose a genetic subclassification on our life table. Individuals in a population may be known to be genetically distinct. Conversely, 'individuals' may actually be asexually produced ramifications of the same genotype. Kays and Harper (1974) recognized this dichotomy and introduced the terms *genet* and *ramet* to avoid confusion. Thus, individuals that are produced asexually (e.g. 'daughter' plants of

buttercups, bulbs, tillers, polyps of *Obelia*, corals) and have the potential for growth independent of the parent are called ramets; and a population of ramets with the same ('maternal') parentage constitutes a *clone*. A genet, on the other hand, is an organism, *however much ramified*, which has arisen from a single zygote—all parts having the same genotype.

## 1.4 Conventional life tables

### 1.4.1 The cohort life table

The most reliable method of determining age-specific mortality and fecundity for a continuously breeding population, or simply one in which generations are overlapping, is to follow the fate of a group of individuals, all born during the same time interval. Such a group is called a *cohort*. The process is essentially a journey from the top left-hand corner of Fig. 1.9 to its bottom right-hand corner, and, in many respects, it is similar to following the fate of an annual

species throughout its yearly cycle. The difference in this case is that each individual has to be recognized and distinguished from those individuals belonging to other cohorts which are in population at the same time. The situation is described diagrammatically in Fig. 1.12 in which individuals are represented by solid lines, ageing with time, and eventually dying (a 'spot' in Fig. 1.12). The cohort of four individuals (born at  $t_0$ ) is observed again at  $t_1$  (when there are two survivors), at  $t_2$  (one survivor), and at  $t_3$  (no survivors).

Plants are ideal subjects for such study, since they are generally sessile and can be tagged or mapped, enabling the fates of individuals to be precisely re-

corded and their reproductive output measured. Law (1975), for instance, followed the fate of a cohort of the annual meadow grass, *Poa annua*, from initial establishment to the ultimate death of the last individual. Recording the number alive at successive time-periods and the number of offspring (seeds) produced per plant, he was able to compile a table of data showing survivorship and fecundity (Table 1.1). The first (left-hand) column gives the age at the beginning of each time interval. Thereafter, only the second and last columns ( $a_x$  and  $B_x$ ) actually contain field data. All other columns are derived from the  $a_x$  column. We can see that this (conventional) life table contains

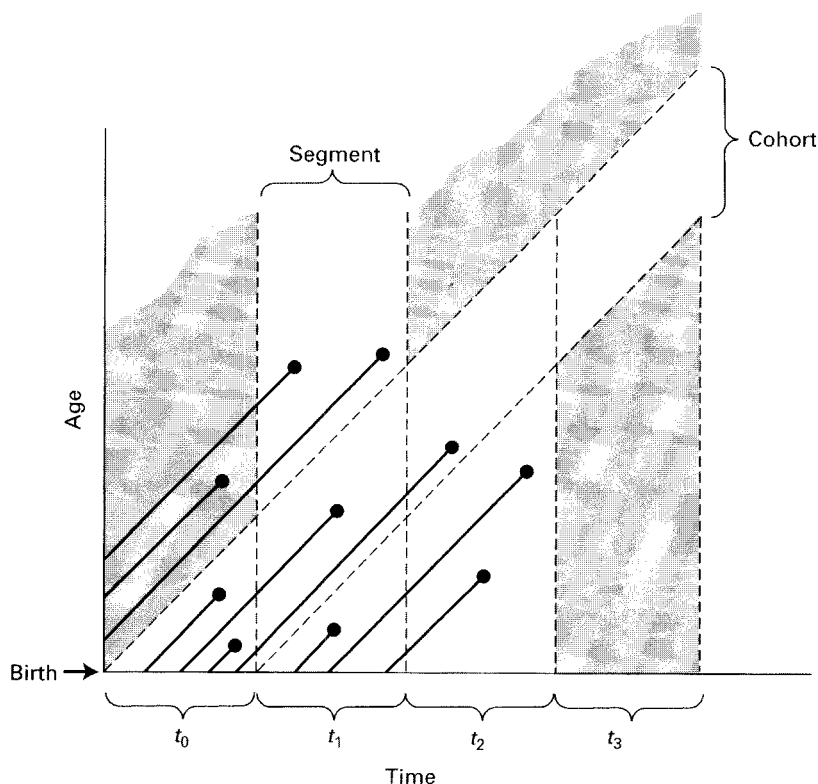


Fig. 1.12 A population portrayed as a series of diagonal lines, each line representing the life 'track' of an individual. As time progresses, each individual ages and eventually dies. Three individuals are born prior to  $t_0$ , four during  $t_0$ , and three during  $t_1$ . To construct a 'fixed' cohort life table, a 'searchlight' is directed into the cohort of individuals born during  $t_0$  and the subsequent development of the cohort is monitored. Two of the four individuals have survived to the

beginning of  $t_1$ ; only one of these is alive at the beginning of  $t_2$ ; and none survives to the start of  $t_3$ . To construct a 'static' life table, the 'searchlight' is directed onto the whole population during a single segment of time ( $t_1$ ). The ages of the seven individuals alive at some time during  $t_1$  may be taken as an indication of the age-specific survival-rates if we assume that the rates of birth and survival are constant. (After Skellam, 1972.)

Table 1.1 A cohort life table for *Poa annua*. (Adapted from Law, 1975.)

| Age<br>(in 3-month<br>periods)<br>$x$ | Number<br>observed alive<br>at each<br>quarter year<br>$a_x$ | Standardized<br>number surviving<br>at the start of age<br>interval $x$<br>$l_x$ | Standardized<br>number dying<br>between $x$<br>and $x + 1$<br>$d_x$ | Mortality-<br>rate<br>$q_x$ | $\log_{10} a_x$ | $\log_{10} l_x$ | $\log_{10} a_x / \log_{10} a_{x+1}$<br>$k_x$ | Average<br>number<br>of seeds per<br>individual<br>aged $x$<br>$B_x$ |
|---------------------------------------|--|--|---|-----------------------------|-----------------|-----------------|--|--|
| 0                                     | 843  | 1000   | 143   | 0.143                       | 2.926           | 3.000           | 0.067  | 0  |
| 1                                     | 722  | 857  | 232   | 0.271                       | 2.859           | 2.933           | 0.137  | 300  |
| 2                                     | 527  | 625  | 250   | 0.400                       | 2.722           | 2.796           | 0.222  | 620  |
| 3                                     | 316  | 375  | 204   | 0.544                       | 2.500           | 2.574           | 0.342  | 430  |
| 4                                     | 144  | 171  | 107   | 0.626                       | 2.158           | 2.232           | 0.426  | 210  |
| 5                                     | 54   | 64   | 46.2  | 0.722                       | 1.732           | 1.806           | 0.556  | 60   |
| 6                                     | 15   | 17.8   | 14.24   | 0.800                       | 1.176           | 1.250           | 0.699  | 30   |
| 7                                     | 3  | 3.56   | 3.56  | 1.000                       | 0.477           | 0.551           |  | 10   |
| 8                                     | 0  | 0  | —   |                             |                 |                 |  | —  |

essentially the same information as the diagrammatic life tables previously described.

The  $a_x$  column summarizes the raw data collected in the field by mapping the positions of 843 *P. annua* plants that arose from naturally sown seeds in a number of metre-square quadrats. From this raw data ' $l_x$ ' values are calculated, by converting the numbers observed at the start of each time interval to the equivalent number that would have occurred had the starting density of the cohort been 1000: e.g.  $l_3 = 316 \times 1000/843 = 375$ . The value of this procedure is that  $l_x$ -values can be compared between populations, or between species, since they do not depend on the actual number of individuals considered in each study. In other words an  $a_0$  value of 843 is peculiar to this set of observations, whereas all studies have an  $l_0$  value of 1000.

To consider mortality more explicitly, the standardized numbers dying in each time interval ( $d_x$ ) must be computed, being simply the difference between  $l_x$  and  $l_{x+1}$ ; e.g.  $d_1 = 857 - 625 = 232$ .  $q_x$ —the age-specific mortality-rate—has also been calculated. This relates  $d_x$  to  $l_x$  in proportional terms, so that, for instance,  $q_2$ —the proportion of the 6-month-old individuals that die in the subsequent 3-month period—is  $250/625$  or  $0.4$ .  $q_x$  can also be thought of as the 'chance of death', and is equivalent to  $(1 - p_x)$  where ' $p$ ' refers to the survival-probability considered previously.

The advantage of the  $d_x$ -values is that they can be summed over a period of time: the number dying in the first 9 months is  $d_0 + d_1 + d_2 (= 625)$ . The disadvantage is that the individual values give no real idea of the intensity or importance of mortality at a particular time. This is because the  $d_x$ -values are larger, the more individuals there are to die.  $q_x$ -Values, on the other hand, are a good measure of the intensity of mortality. Thus, in the present example, it is clear from the  $q_x$  column that the mortality-rate rose consistently with increasing age; this is not clear from the  $d_x$  column. The  $q_x$ -values, however, have the disadvantage of not being liable to summation:  $q_0 + q_1 + q_2$  does not give us the overall mortality-rate for the first 9 months. These advantages are combined, however, in the penultimate column of Table 1.1 in which ' $k$ '-values (Haldane, 1949; Varley & Gradwell, 1970) are listed.  $k_x$  is defined, simply, as  $\log_{10} a_x - \log_{10} a_{x+1}$  (or, equivalently,  $\log_{10} a_x / a_{x+1}$ ), and is sometimes referred to as 'killing-power'. Like  $q$ ,  $k$ -values reflect the intensity or rate of mortality, and, in the present case, they increase consistently with age. But, unlike  $q$ , summing the  $k$ -values is a meaningful procedure. Thus the killing-power or  $k$ -value of the first 9 months is  $0.067 + 0.137 + 0.222 = 0.426$ , which is also the value of  $\log_{10} a_0 - \log_{10} a_9$ . Note, furthermore, that the  $k_x$ -values can be computed from the  $l_x$ -values as well as the  $a_x$ -values; and that, like  $l_x$ ,

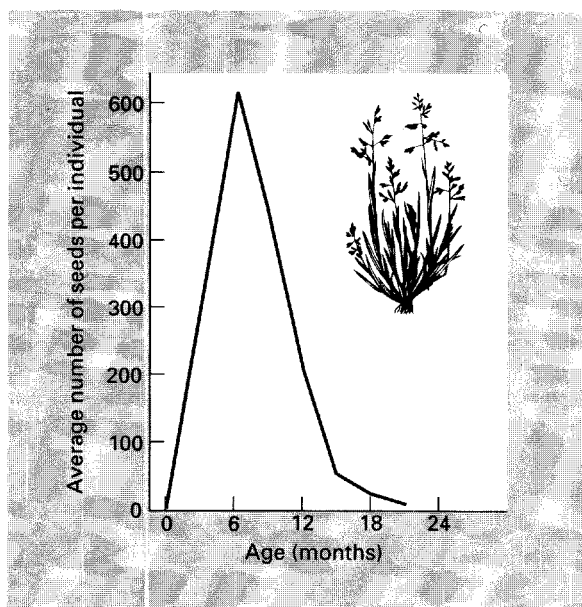


Fig. 1.13 Age-specific fecundity ( $B_x$ ) for the annual meadow grass *Poa annua*. (Data from Law, 1975.)

$k_x$  is standardized and is, therefore, appropriate for comparing quite separate studies.  $k$ -values will be of considerable use to us in later chapters.

The age-specific patterns of fecundity and mortality have been plotted in Figs 1.13 and 1.14. Figure 1.13

indicates quite clearly an initial sharp rise in fecundity reaching a peak at 6 months, followed by a gradual decline until the death of the last individual after 2 years. Figure 1.14 illustrates a single pattern in three different ways. Figure 1.14a is 'survivorship curve'— $\log_{10} l_x$  plotted against age—while Fig. 1.14b contains two mortality curves,  $q_x$  and  $k_x$ , plotted against age. All show a consistent rise in the rate of mortality, leading to an increasingly rapid decline in survivorship. Of the three, Fig. 1.14a—the survivorship curve—probably shows this most clearly.

The use of logarithms in the survivorship curve deserves further comment. Consider, for instance, the halving of a population over 1 unit of time, in one case from 100 to 50 individuals, and in another case from 10 to five individuals. In both cases there has been a reduction by half, i.e. the rate or probability of death *per individual* (usually referred to as the 'per capita rate') is the same. Nevertheless, the slope of an *arithmetic* survivorship curve would be  $-50$  in the first case but  $-5$  in the second. With logarithmic survivorship curves, however, the slopes in these two, equivalent cases are identical. In fact, equivalent advantages are gained by the use of  $k_x$ -values: being based on logarithms, they, too, allow recognition of cases in which per capita rates of mortality are the same. Moreover, logarithms also indicate when per

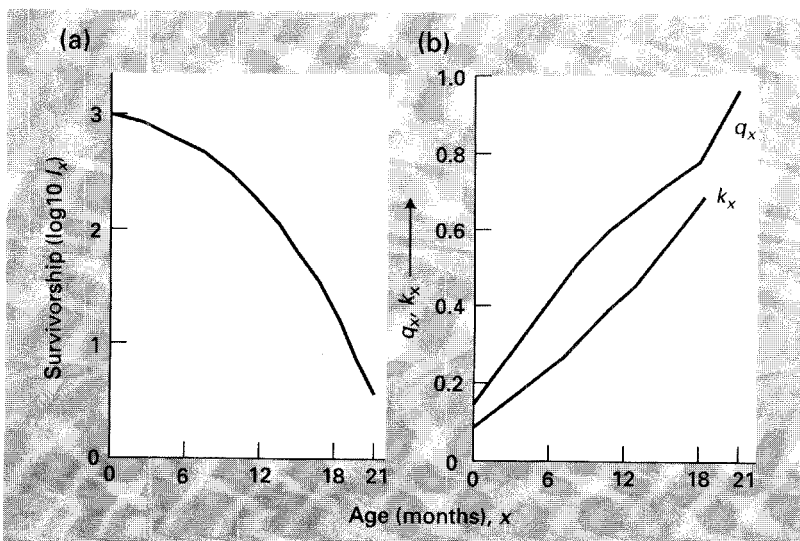


Fig. 1.14 (a) Age-specific survivorship ( $\log_{10} l_x$ ), and (b) age-specific mortality-rates ( $q_x$ ) and killing-powers ( $k_x$ ) for the annual meadow grass *Poa annua*. (Data from Law, 1975.)

capita rates of *increase* are identical. 'Log numbers' should therefore be used in preference to 'numbers' when numerical change is being plotted.

#### 1.4.2 The static life table

Unfortunately, it is not always possible to monitor the dynamics of a population by constructing a 'fixed cohort' life table. It is, in fact, rarely possible with natural populations of animals, since the individuals are often highly mobile, highly cryptic or both. There is, however, a rather imperfect alternative, which is also illustrated diagrammatically in Fig. 1.1.2. It involves examining the age-structure of the whole population at one particular time, or, since these things cannot be done instantaneously, during one short 'segment' of time.

As an example, we can consider the results, reported by Lowe (1969), of an extensive study of the red deer (*Cervus elaphus*) on the small island of Rhum, Scotland. Each year from 1957 onwards, Lowe and his co-workers examined every one of the deer that was shot under the rigorously controlled conditions of this nature reserve. They also made extensive searches for the carcasses of deer that had died from natural causes. Thus, they had access to a large proportion of the deer that died from 1957 onwards. Deer can be reliably aged by the examination of tooth replacement, eruption and wear, and Lowe and his co-workers carried out such examinations on all of the dead deer. If, for instance, they examined a 6-year-old deer in 1961, they were able to conclude that, in 1957, this deer was alive and 2 years old. Thus, by examining carcasses, they were able to reconstruct the age-structure of the 1957 population. (Their results did not represent the total numbers alive, because some carcasses must have decomposed before they could be discovered and examined.) Of course, the age-structure of the 1957 population could have been ascertained by shooting and examining large numbers of deer in 1957; but, since the ultimate aim of the project was enlightened conservation of the deer, this method would have been somewhat inappropriate.

Lowe's raw data for red deer hinds are presented in

column two of Table 1.2. As expected, there were many young deer and rather fewer old deer, but we can treat these raw data as the basis for a life table *only* if we make a certain set of assumptions. We must assume that the 59 6-year-old deer alive in 1957 were the survivors of 78 5-year-old deer alive in 1956, which were themselves the survivors of 81 4-year-olds in 1955, and so on. In other words, we must assume that the numbers of births and age-specific survival-rates had remained the same from year to year, or, equivalently, that the  $a_x$  column of Table 1.2 is essentially the same as *would* have been obtained if we *had* followed a single cohort. Having made this assumption,  $l_x$ ,  $d_x$  and  $q_x$  columns have been constructed. It is clear from Table 1.2, however, that our assumption is false. The 'cohort' actually increases in size from years 6 to 7 and 14 to 15, leading to 'negative' deaths and meaningless mortality-rates. The pitfalls of constructing such 'static' life tables are, therefore, amply illustrated.

Nevertheless, such data are by no means valueless. Lowe's aim was to provide a *general* idea of the population's age-specific survival-rate (and birth-rate) prior to 1957 (when culling of the population began), and then to compare this with the situation after 1957. He was more concerned with general trends than with the particular changes occurring from one year to the next. He therefore 'smoothed out' the variations in population size between the ages of 2–8 and 10–16, and *created* a steady decline in both of these periods. The results of this process are shown in the final five columns of Table 1.2, and the mortality schedules are plotted in Fig. 1.15. They do, indeed, provide the general picture Lowe required: there is a fairly gentle but increasing decline in survivorship up to year 8, followed by 2 years of very heavy mortality, and then a return to a gentler, though again increasing, decline.

Moreover, by examining the internal reproductive organs of the hinds, Lowe was also able to derive a sequence of age-specific birth-rates. This is shown in the sixth column of Table 1.2, and illustrated in Fig. 1.16. There is, clearly, an initial pre-reproductive period of 2 years, followed by a sudden increase in birth-rate which is maintained for 3 years. There is then a period of 4 years during which the birth-rate is



Table 1.2 A static life table for red deer. (From Lowe, 1969.)

| $x$<br>(years) | $x_x$ | $l_x$ | $d_x$ | $q_x$ | $B_x$ | Smoothed |       |       |                 |       |
|----------------|-------|-------|-------|-------|-------|----------|-------|-------|-----------------|-------|
|                |       |       |       |       |       | $l_x$    | $d_x$ | $q_x$ | $\log_{10} l_x$ | $k_x$ |
| 1              | 129   | 1000  | 116   | 0.116 | 0     | 1000     | 137   | 0.137 | 3.000           | 0.064 |
| 2              | 114   | 884   | 8     | 0.009 | 0     | 863      | 85    | 0.097 | 2.936           | 0.045 |
| 3              | 113   | 876   | 48    | 0.055 | 0.311 | 778      | 84    | 0.108 | 2.891           | 0.050 |
| 4              | 81    | 625   | 23    | 0.037 | 0.278 | 694      | 84    | 0.121 | 2.841           | 0.056 |
| 5              | 78    | 605   | 148   | 0.245 | 0.302 | 610      | 84    | 0.137 | 2.785           | 0.064 |
| 6              | 59    | 457   | -47   | —     | 0.400 | 526      | 84    | 0.159 | 2.721           | 0.076 |
| 7              | 65    | 504   | 78    | 0.155 | 0.476 | 442      | 85    | 0.190 | 2.645           | 0.092 |
| 8              | 55    | 426   | 232   | 0.545 | 0.358 | 357      | 176   | 0.502 | 2.553           | 0.295 |
| 9              | 25    | 194   | 124   | 0.639 | 0.447 | 181      | 122   | 0.672 | 2.258           | 0.487 |
| 10             | 9     | 70    | 8     | 0.114 | 0.289 | 59       | 8     | 0.141 | 1.771           | 0.063 |
| 11             | 8     | 62    | 8     | 0.129 | 0.283 | 51       | 9     | 0.165 | 1.708           | 0.085 |
| 12             | 7     | 54    | 38    | 0.704 | 0.285 | 42       | 8     | 0.198 | 1.623           | 0.092 |
| 13             | 2     | 16    | 8     | 0.500 | 0.283 | 34       | 9     | 0.247 | 1.531           | 0.133 |
| 14             | 1     | 8     | -23   | —     | 0.282 | 25       | 8     | 0.329 | 1.398           | 0.168 |
| 15             | 4     | 31    | 15    | 0.484 | 0.285 | 17       | 8     | 0.492 | 1.230           | 0.276 |
| 16             | 2     | 16    | —     | —     | 0.284 | 9        | 9     | 1.000 | 0.954           | —     |

higher still, followed by a return to the previous level. It is interesting to note that the period of high birth-rates is immediately followed by a period of high mortality-rates, an apparent ‘cost of reproduction’.

1.4.3 Resumé

Conventional (as opposed to diagrammatic) life tables are the medium through which age-specific schedules

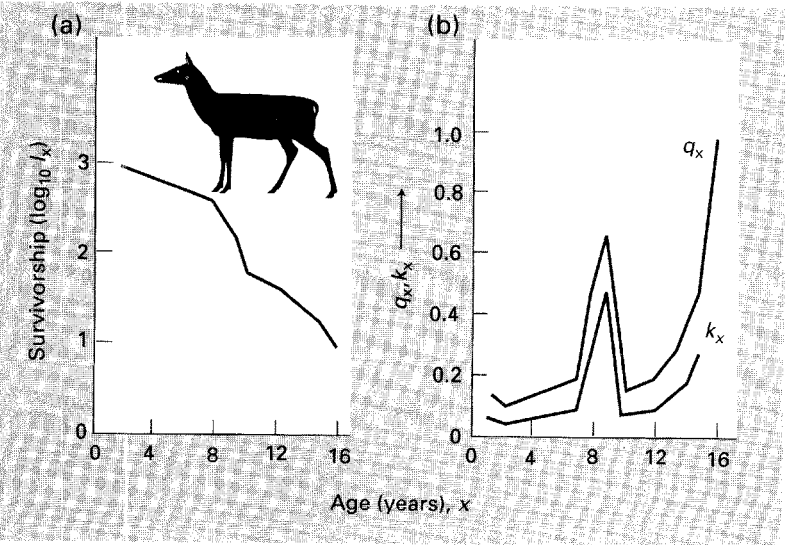


Fig. 1.15 (a) Age-specific survivorship ( $\log_{10} l_x$ ), and (b) age-specific mortality-rates ( $q_x$ ) and killing-powers ( $k_x$ ) for the red deer, *Cervus elaphus*. (Data from Lowe, 1969.)

of death (and birth) can be constructed, and it is obvious that the compilation of such information is vital if the dynamics of populations are to be understood. These life tables can be of two quite separate types (see Fig. 1.12).

The *fixed cohort* (or 'dynamic', or 'horizontal') life table is derived by actually following a cohort of individuals from birth to extinction. It provides reliable information on that cohort; but its construction may be beset by practical difficulties, which in certain cases will be insuperable.

The *static* (or 'time-specific', or 'vertical') life table, conversely, is derived by estimating the age structure of a population at one point in time. It is equivalent to a fixed cohort life table only when the survival-rates in the population are constant. Otherwise the static life table compounds and confuses two quite separate things: the age-specific changes in birth- and mortality-rate, and the year-to-year variations in these rates in the past. Nevertheless, it can provide a general idea of age-specific birth- and mortality-rates in a population, which is particularly valuable when a fixed cohort life table *cannot* be derived.

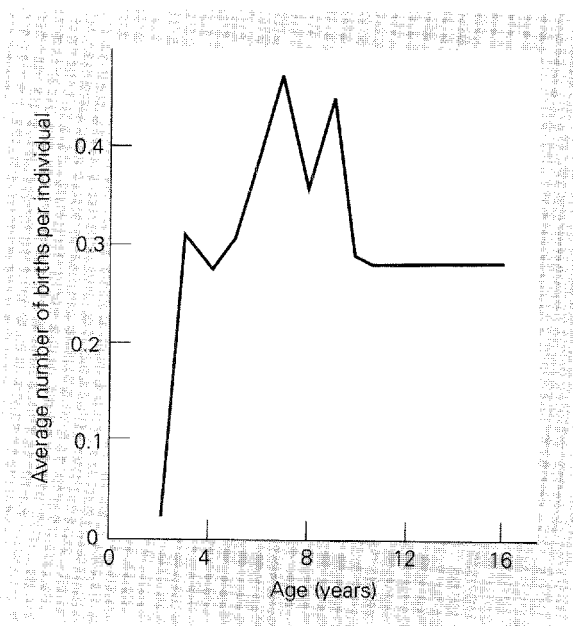


Fig. 1.16 Age-specific fecundity for the red deer *Cervus elaphus*. (Data from Lowe, 1969.)

It should also be stressed that in either case it is often necessary to collect life-table data over a period of time for a number of generations. This allows the natural variability in the rates of birth and survival to be monitored and assessed.

## 1.5 Some generalizations

One of the reasons for using life tables to monitor these age-specific rates is that this allows us to discover patterns of birth and mortality which are repeated in a variety of species in a variety of circumstances. In turn, this allows us, hopefully, to uncover the common properties shared by these various populations, leading ultimately to a deeper understanding of population dynamics *in general*. Age-specific mortality-rates were classified by Pearl (1928), and his classification is illustrated in Fig. 1.17 in the form of survivorship curves. It is very difficult to generalize about the shape of survivorship curves, not least because they are a reflection of the particular habitat conditions in which the population was observed, and the actual densities of populations. Figure 1.18 illustrates the range of curves for a sand dune annual plant in natural populations in similar habitat varying in density and

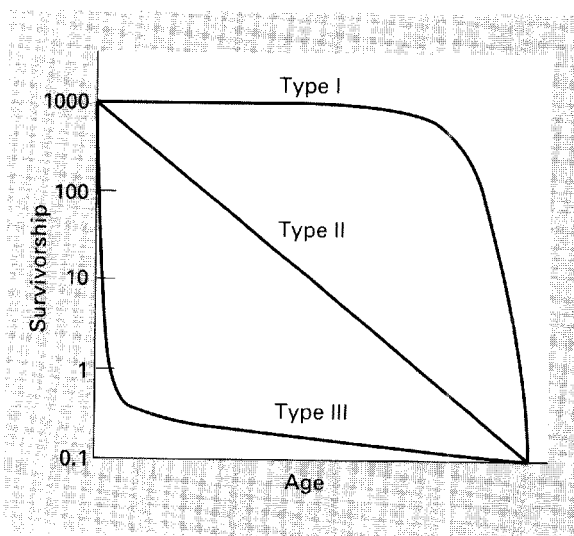


Fig. 1.17 Hypothetical standard survivorship curves. (After Pearl, 1928.) For further discussion, see text.

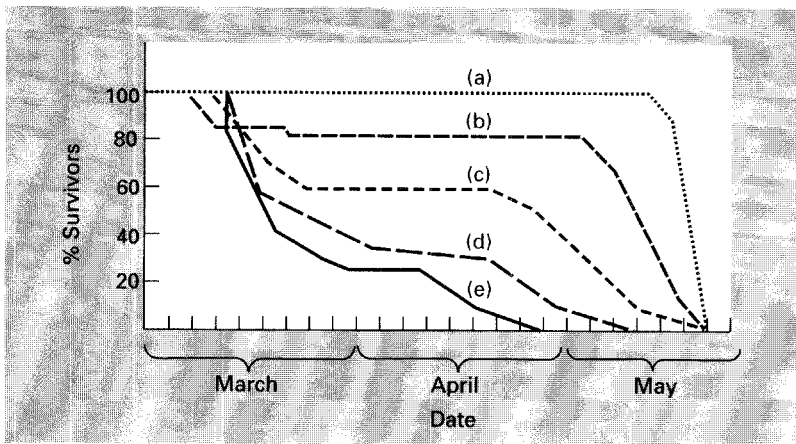


Fig. 1.18 Survivorship curves in natural populations of *Erophila verna* occurring at differing densities ( $\times 10^3 \text{ m}^{-2}$ ) (a) 1–2; (b) 5–10; (c) 15–10; (d) 35–50; and (e) >50. (After Symonides, 1983.)

we can see that a spectrum of curves may occur. However, Pearl argued that we can recognize three broad types. The first—epitomized perhaps, by humans in the developed world or cosseted animals in a zoo—describes the situation in which mortality is concentrated at the end of the maximum life span. In the second, the probability of death remains constant with age, leading to a linear decline in survivorship. This typically occurs in the buried seed populations of plants. In the third type there is extensive early mortality, but those that remain have a high rate of survival subsequently. This is true, for instance, of many marine fish which produce millions of eggs of which very few survive to become adults.

The difficulty with Pearl's generalizations is that as a cohort ages it may well follow, successively, more than one type of survivorship curve. It is now known, for instance, that for many grassland plants the survivorship curve of seedlings establishing into adults is type 3, whereas that of the adults themselves is type 2.

Generalizations regarding age-specific birth-rates are, in many ways, more straightforward. The most basic distinction, perhaps, is between species which are *semelparous*, reproducing only once, and those which are *iteroparous*, reproducing many times. In the botanical literature, these terms are referred to as *monocarpic* and *polycarpic*, respectively. In either case there is likely to be a *pre-reproductive period*, which can, of course, vary in length (cf. Figs 1.16 & 1.19). Age-specific fecundity may then rise, either to a peak (*P.*

*annua*, see Fig. 1.13), or to a plateau (the deer in Fig. 1.19) or tend to increase with age in trees as size increases (Fig. 1.20). As Fig. 1.16 shows, however, many species combine elements of the two in a more complex pattern.

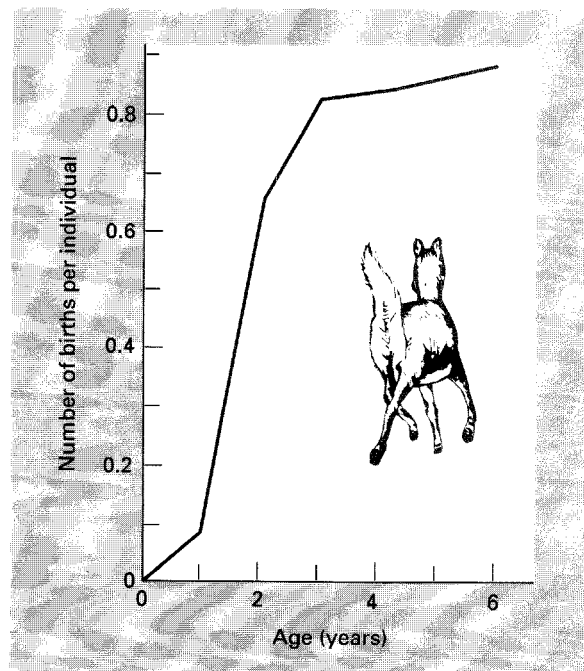


Fig. 1.19 Age-specific fecundity for white-tailed deer *Odocoileus hemionus* in Michigan. (Data from Eberhardt, 1960.)

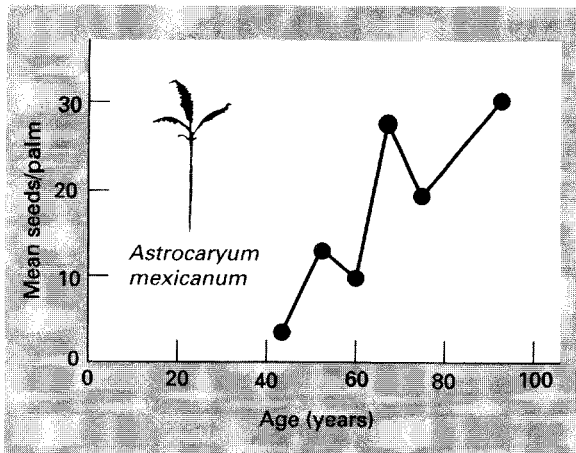


Fig. 1.20 Age-dependent seed production in the tree palm *Astrocarium mexicanum*. (After Sarukhan, 1980.)

Finally, certain restricted generalizations can be made regarding population size itself. It is indisputable that all populations vary in size: temporal fluctuations are the universal rule. But at the same time it is equally true that these fluctuations are usually limited in amplitude. Populations rarely increase in size so much that they utterly overrun their environment; and even localized extinctions, though by no means unknown, are also comparatively rare. Thus, population size, and the processes affecting it, are variable—but of limited variability. One of the major aims in the study of population dynamics is to understand these limitations, and this is the topic to which we shall turn in the next chapter. Before doing so we must first consider the implications of the ways in which some plants and animals grow for our means of describing populations.

## 1.6 The modular growth of organisms

Having concentrated on what different types of species population may have in common, we now turn to one crucial respect in which they may differ. A major distinction amongst species of both plants and animals lies in the organization and differentiation of tissues. This fundamental distinction divides organisms according to their growth form into those that are *unitary* and those that are *modular* (Harper & Bell,

1979; Harper, 1981). Most animals are unitary organisms. Development from the zygote (the fertilized egg) through to the adult involves an irreversible process of growth and tissue differentiation leading to organ development according to a highly regulated schedule. Conversely, most plants are modular. Growth and differentiation are normally initiated in 'meristems' at the apices of shoots and roots (Esau, 1953). Cell divisions occur in these meristems, and they result in root and shoot elongation and the laying down of further meristems. Growth from meristems in this way unaccompanied by any further differentiation leads to a repetitive or reiterative modular structure in the plant body (see Gottlieb, 1984 for a succinct discussion). Botanically, a 'module' is an axis (essentially a length of tissue) with an 'apical meristem' at its distal end. The axis is subdivided by nodes at which leaves, axillary meristems and vegetative outgrowths (e.g. tendrils) may occur. If and when the apical meristem differentiates into a terminal flower, extension growth of the axis ceases.

Modular organisms increase in size by a programme of growth and development that is structurally and functionally repetitive; unitary organisms by contrast do not. The distinction, however, is not simply one between animals and plants. In colonial animals such as corals, hydroids, bryozoans and colonial ascidians similar modular identities can be seen (Rosen, 1979). We saw in section 1.3.5 that both corals and buttercups increased in size through the addition of successive segments or modular units. Thus, put simply, the buttercup becomes larger as additional stolons and ramets are produced while the coral becomes larger as polyps grow and bud. Each increment in growth can be measured by the number of modules produced in a period of time. This feature has proved invaluable to plant demographers in the construction of static life tables; since in some species at least, the age of an individual plant may be deduced from persisting morphological or anatomical features. The method has been used in investigating survivorship in the Mexican tree palm (*Astrocarium mexicanum*) and also in examining clonal growth in rhizomatous species. *Polygonatum verticillatum* is a herb of Scandinavian and Danish forests which annually produces an above-

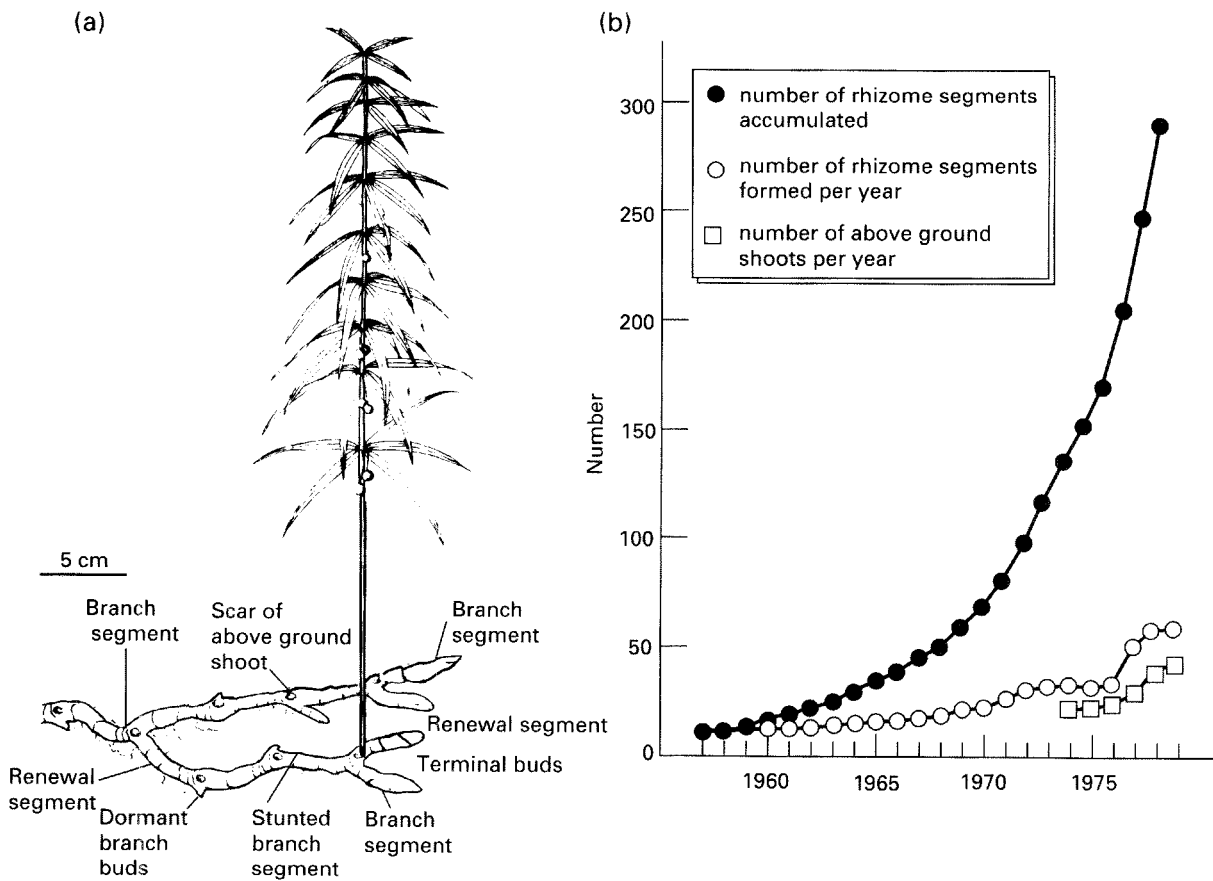


Fig. 1.21 (a) The morphology of the rhizomatous perennial *Polygonatum verticillatum*. (b) Exponential growth of rhizome segments in a clone of *P. verticillatum*. (After Tybjerg & Vestergaard, 1992.)

ground shoot that dies in the autumn leaving a distinct below-ground scar on the rhizome. The growth form enabled Tybjerg and Vestergaard (1992) to be able to age an excavated rhizome system (Fig. 1.21a) retrospectively over a 20-year period. Careful mapping indicated that direction of growth was centrifugal from the initial (seedling) starting point and the cumulative number of rhizome segments increased exponentially (Fig. 1.21b). This arose because the rhizomes bifurcated in a systematic manner with the number of new branches increasing gradually as the plant aged.

Three important demographic consequences arise from recognizing the modular construction of higher terrestrial plants and colonial animals. The first is that the addition of modules tends to lead to a branched structural form. Generally, this is because of the placement of meristems in plants at acute angles to the main axis, which continue growth when extension of the parental axis ceases. The exact architecture of the organism will depend on: (i) whether modules vary in form, as in the short and long branches of trees or the vegetative and generative (i.e. reproductive) polyps of hydroids; (ii) their rate of production; and (iii) their position relative to one another. Nevertheless, the overall form of the organism is a *colony* of repeating modules. The form is important demographically since size and shape will influence the nature of interactions amongst static organisms (Horn, 1971).

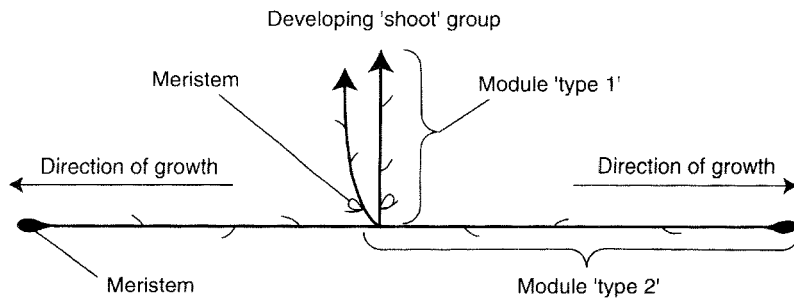


Fig. 1.22 A schematic view of modular growth in a plant that displays two types of module in its constructional organization. Natural cloning results from the fragmentation of either type of module. Module 'type 1' is a 'shoot' bearing foliage leaves and one meristem capable of

generating either 'type 1' or 'type 2' modules. Module 'type 2' is a horizontal stem (rhizome or stolon) bearing a meristem with the potential to give rise to a 'type 1' module, axillary meristems and roots. (After Harper & Bell, 1979.)

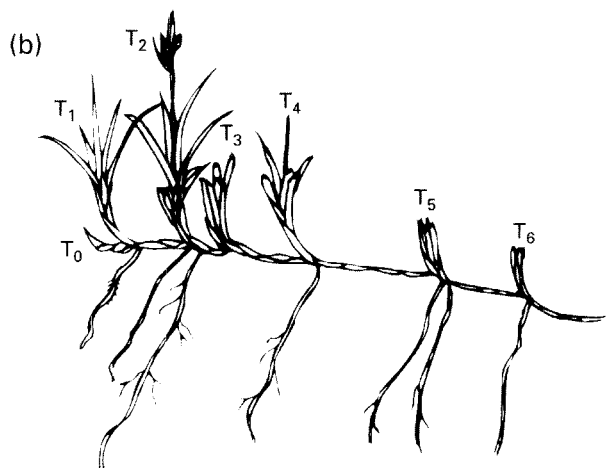
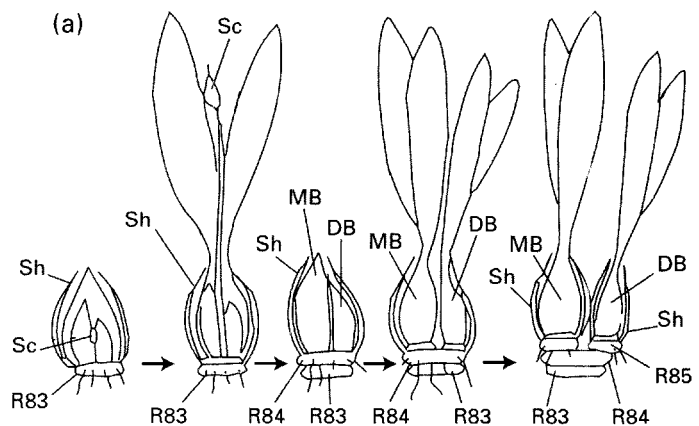
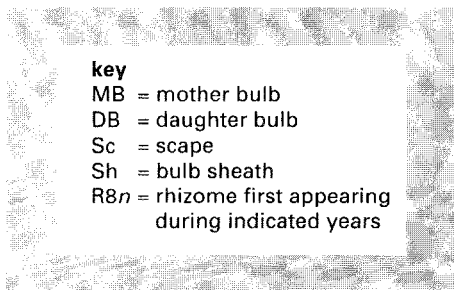


Fig. 1.23 (a) Bulb division and sequential development of daughter ramets in *Allium tricoccum*. (After Nault & Gagnon, 1993.)

(b) Rhizomatous growth in *Carex bigelowii*. (After Jónsdóttir & Callaghan, 1988.)

Whether an individual creeping plant, for instance, presents a compact as opposed to diffuse arrangement of shoots may have important consequences in competitive interactions with neighbours as will the branching structure influence interactions amongst the crowns of trees.

Second, removal of modules (through damage, herbivory or predation for instance) may harm an organism but not kill it. A modular architectural arrangement of relatively autonomous meristems allows lost parts to be reiterated. The potential for this very much depends upon the degree of permanent physiological and morphological differentiation that has already occurred. Removal of vegetative tillers from a grass plant will often lead to the reiteration of the tiller module; removal of an inflorescence (a module that has differentiated into a sexually generative structure) may not—often because of the absence of further growth points. Conversely, in unitary organisms although tissue regeneration does occur, removal of a whole organ will precipitate death.

A third consequence arises from the fact that modularity affords the opportunity of natural cloning (Harper, 1985). Natural cloning arises when a genet fragments and the ramets establish into physiologically independent parts (Fig. 1.22). This is only possible when meristems at nodes retain totipotency: the ability to produce both shoots and roots. Fragmentation may arise through physical agencies (e.g. sand movement in the sand sedge *Carex arenaria*), the trampling and grazing of herbivores (in rhizomatous grasses), or it may be genetically determined (as in *Ranunculus repens*; Bell & Tomlinson, 1980). The important demographic point is that whatever the agency, it may lead to a colony of physiologically independent plants of the same genotype which are potential competitors. The extent to which the ramets of a clone constitute truly independent individuals when they retain apparent physical connections requires careful scrutiny. In some cases the true disjunction of individuals is an age/size-dependent process (as in *Allium tricoccum*; Fig. 1.23a), but is more problematic in perennial grasses (Fig. 1.23b).

These observations on modularity have prompted the suggestion that the fundamental equation of

population biology (equation 1.1 above) applies not only at the level of the genet (expressed through the growth of the clone as a whole) but also at the (lower) modular level (Harper, 1977). Harper and Bell (1979) argue then that the study of the dynamics of modules themselves is an essential component in describing the population ecology of modular organisms and can be applied down to the level of individual leaves (Harper, 1989). Demographic approaches to modular dynamics have employed the same techniques that we have examined earlier for populations of unitary organisms. Thus, Fig. 1.24 shows a diagrammatic life table for a population of meristems on a *Fuchsia* plant. As the plant grows, some meristems develop into shoots which may be vegetative (branches bearing new meristems) or generative (branches bearing inflores-

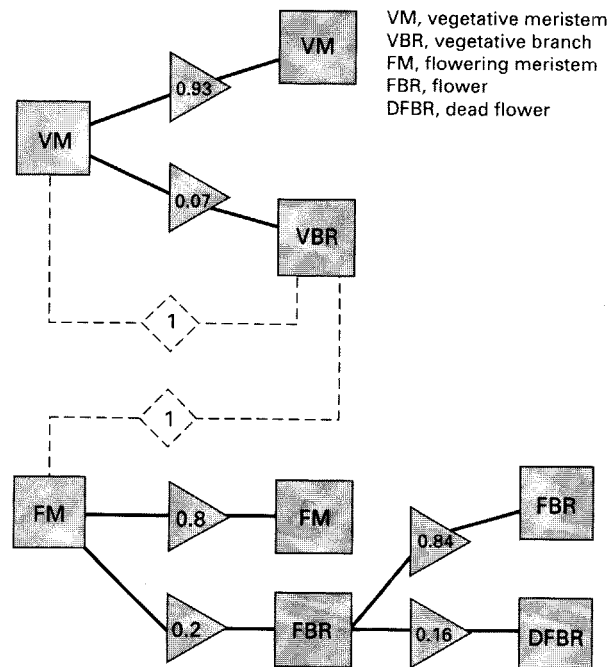


Fig. 1.24 Transitions occurring over a time period amongst meristems in Royal Velvet, a cultivar of *Fuchsia*.

Measurements were made 75 days after planting on the main shoot when plants were growing exponentially. At this stage of growth a constant fraction of vegetative meristems become vegetative branches which in turn produce one vegetative and one flower meristem. (Data from Porter, 1983a.)

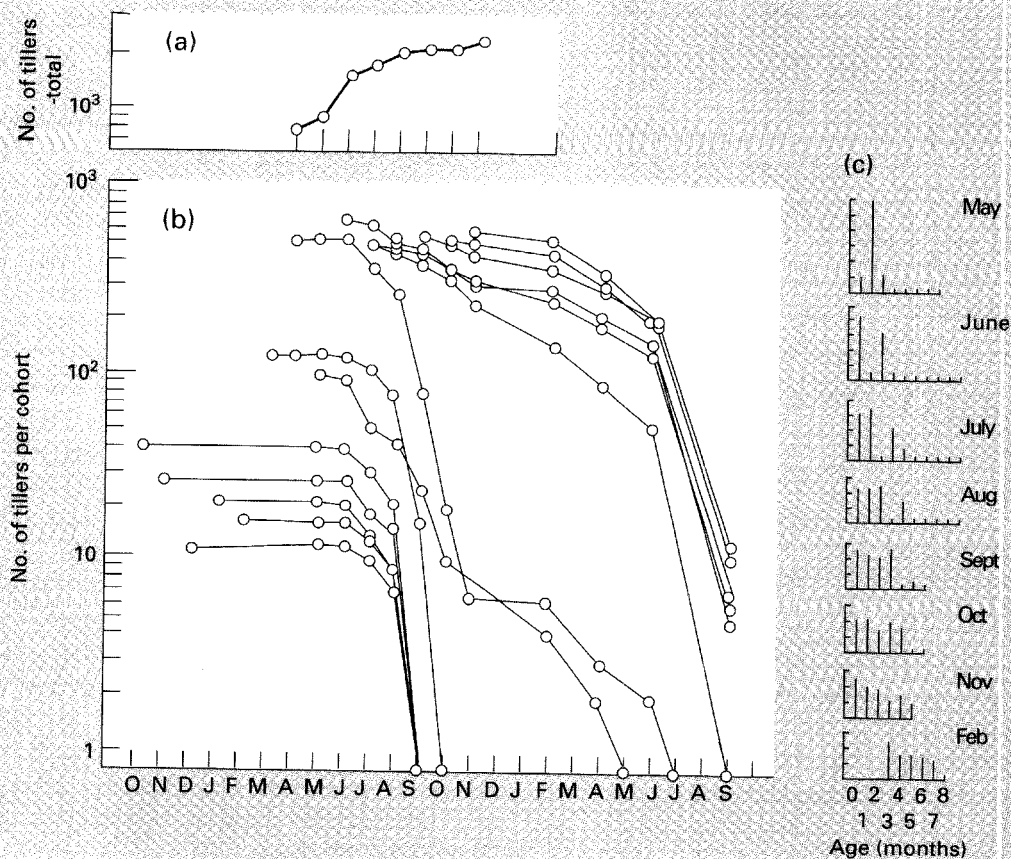


Fig. 1.25 Flux in tillers in *Phleum pratense*: (a) the total number of living tillers; (b) survivorship curves of successive monthly cohorts of tillers; (c) tiller age structure at successive monthly periods (each ordinate division is 10%). Data were gathered from 40 plants each grown from seed in soil in separate 20-cm diameter pots. (From Langer, 1956; after White, 1980.)

cences), some meristems remain dormant, whilst others abort. The transitions given in Fig. 1.24 are those occurring during growth in an unrestricted environment once plants have started flowering. Death of meristems, whether vegetative or flowering, is absent and only occurs when flowers (the products of generative meristems) senesce.

Flux in modules, however, can be much more noticeable in other species. Langer (1956) followed the

fate of grass tillers on individual timothy plants (*Phleum pratense*) over a period of 2 years. His data (Fig. 1.25) illustrate that tiller births and deaths are an intrinsic feature of the life of an individual plant. Whilst the size of cohorts recruited each month was seasonally dependent, the pattern of mortality in cohorts was remarkably similar, following a type 1 survivorship curve. This mortality mainly resulted from the 'monocarpic' nature of tillers (the production of an inflorescence on a tiller is followed inevitably by tiller death) but also occurred amongst non-generative tillers when recruitment of tillers was at its highest in June/July. Tillers formed in April and May were either annual (flowering in the following August and September) or biennial, remaining vegetative over winter and flowering the next year. This resulted in the stepped survivorship curves seen in Fig. 1.25.



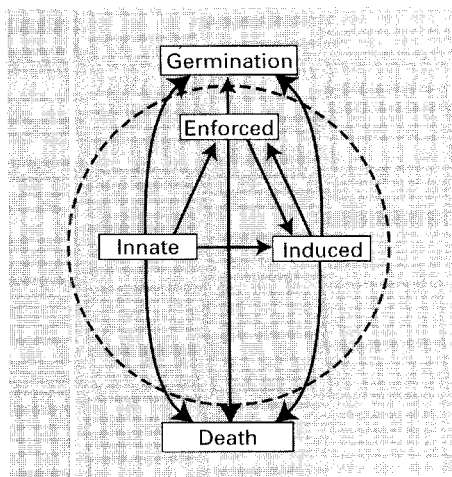


Fig. 1.26 The interrelationships between states of seed dormancy in a buried seed population. Arrows indicate direction of transition according to definitions of dormancy state (see text for details). (After Sagar & Mortimer, 1976.)

In conclusion, it is clear that in describing a population we must carefully define the individual. This in part will depend on the nature of the scientific enquiry, but more often than not it will be determined by the growth form of the organism.

## 1.7 Buried seed banks

Although we have referred in passing to the existence of buried seed banks (see section 1.5), it is important to recognize that populations of both terrestrial and aquatic plants may differ from animal populations in this additional respect. In many plant species, a very

large fraction of the total population may be present as dormant individuals within the soil profile, such that the number of live plants above ground gives a very poor reflection of the true population size.

Thompson and Grime (1979) distinguished between two classes of species possessing buried seed banks: those with seeds that have limited longevity, specifically no longer than a year following dispersal and often no longer than the species generation time—*transient* banks; and those in which a proportion of seeds survives in a dormant state for more than one generation time—*persistent* banks. Seed survival for long periods in the soil is controlled by three types of dormancy mechanism (Harper, 1977). *Enforced dormancy* arises where there is the absence of at least one exogenous factor. Thus insufficient water availability or burial at depth away from light prohibits germination which occurs on removal of the limiting factor(s). Conversely, *innate dormancy* is an endogenous physiological or morphological condition possessed by a seed at the time of dispersal from the mother plant and which is broken by a subsequent appropriate cue—for instance passage through the gut of an animal or experience of a temperature shift. Finally *induced dormancy* is a responsive form of dormancy that arises as a consequence of an environmental stimulus. Release from this form of dormancy arises on receipt of a further stimulus which may well be of a seasonal nature (Roberts, 1972). Thus dormancy induced by low soil temperatures in autumn that herald winter may be broken by elevated temperatures in spring. The dormancy structure of a buried seed population may be classified in this tripartite manner as illus-

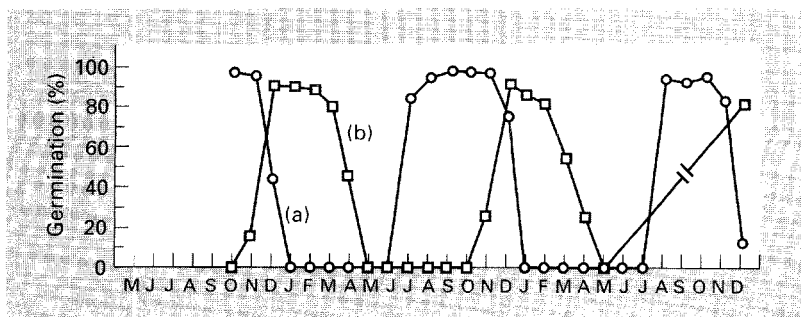


Fig. 1.27 Seasonal changes in induced seed dormancy in two annuals; (a) *Arabidopsis thaliana*, and (b) *Ambrosia artemisiifolia*. Buried seeds were retrieved each month and germinated at their respective optimum temperature. (After Baskin & Baskin, 1980, 1983.)

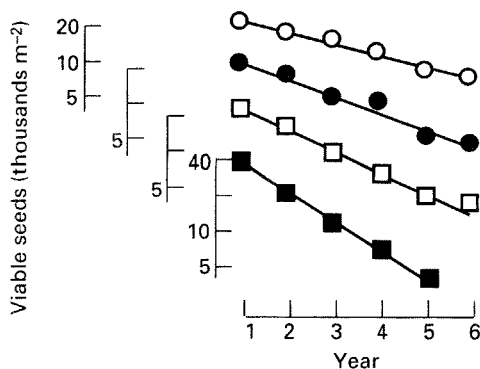


Fig. 1.28 The decrease in the number of viable dormant seeds (a four species mixture) buried in soil, disturbed at differing frequencies throughout the year. Note numbers are presented on a logarithmic scale. ○, undisturbed soil; □, soil cultivated twice a year; ●, soil cultivated four times a year; ■, soil cultivated under a cropping rotation. (After Roberts & Dawkins, 1967.)

trated in Fig. 1.26 and it is possible with the appropriate techniques to estimate the proportion in each category (Baskin & Baskin, 1980). Repeated sampling has shown that annual cycles in dormancy status occur in viable seed populations (Fig. 1.27) and if there is loss by germination and no recruitment of newly dispersed seed, then the seed bank declines. Meticulous studies have shown that the rate of this loss tends to be constant (Fig. 1.28) for a particular habitat when viewed on an annual basis although losses may be concentrated at particular seasons of the year. In some temperate plants the longevity of buried seed may be considerable—in poppies for instance in excess of 80 years. In contrast, in many tropical species it is often restricted to 15–20 months (Garwood, 1989).